

are offered here. It appears that the plant reappeared (very scantily, indeed) in some of the denuded areas during the summer, and that the rhizomes were sometimes still present under the mud in the old meadows, intact, and perhaps viable. It is certain that in no considerable area did the plant, remaining dormant during early summer, reappear to full luxuriance by September.—W. R. T.

#### EXPLANATION OF PLATE 274

Fig. 1. *SPHACELARIA PLUMIGERA*, tip of axis showing distichous ramuli,  $\times 18.5$ ; fig. 2. *TILOPTERIS MERTENSII*, portion of small branch showing ultimate ramuli with monosporangia,  $\times 16.5$ ; fig. 3. *TILOPTERIS MERTENSII*, portion of main axis showing habit,  $\times 3.2$ ; fig. 4. *SPHACELARIA PLUMIGERA*, portion of plant showing habit,  $\times 7.1$ .

### THE DISTRIBUTION OF *IRIS VERSICOLOR* IN RELATION TO THE POST-GLACIAL GREAT LAKES<sup>1</sup>.

EDGAR ANDERSON

IN connection with a study of geographical differentiation in two species of *Iris* (Anderson 1928), an attempt has been made to work out their distribution in as great detail as possible. While the survey is not yet completed, it gives promise of contributing useful evidence as to vegetational changes in glacial and post-glacial times.

*Iris versicolor* is a northern species, its distribution being roughly that of the northern coniferous forest. *Iris virginica* is a southern species which spreads up from the Gulf and the southern coastal plain to Virginia, Ohio, southern Michigan, and central Minnesota. At the western limits of their ranges, where the transition between northern coniferous forest and deciduous forest is a sharp one, the range of *Iris versicolor* coincides exactly with that of the white pine (*Pinus Strobus*). Figure 1. is compiled from my own collections and from records very kindly sent me by Prof. F. K. Butters of the University of Minnesota and by Prof. N. C. Fassett of the University of Wisconsin. It shows the western distribution of *Iris versicolor* in relation to that of the northern forest. Eastward, in Michigan, Ontario and Ohio, where the boundaries of the northern forest become less clearly defined, the ranges of *Iris versicolor* and *Pinus Strobus* show greater deviation though they are still essentially the same.

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A very similar situation has been reported by Butters (1927) in his careful study of the varieties of *Maianthemum canadense*. He finds that in Minnesota the two varieties of *Maianthemum* are so sharply separated that they might be considered as good species were it not for the fact that they have become hopelessly intermingled along the Atlantic seaboard.

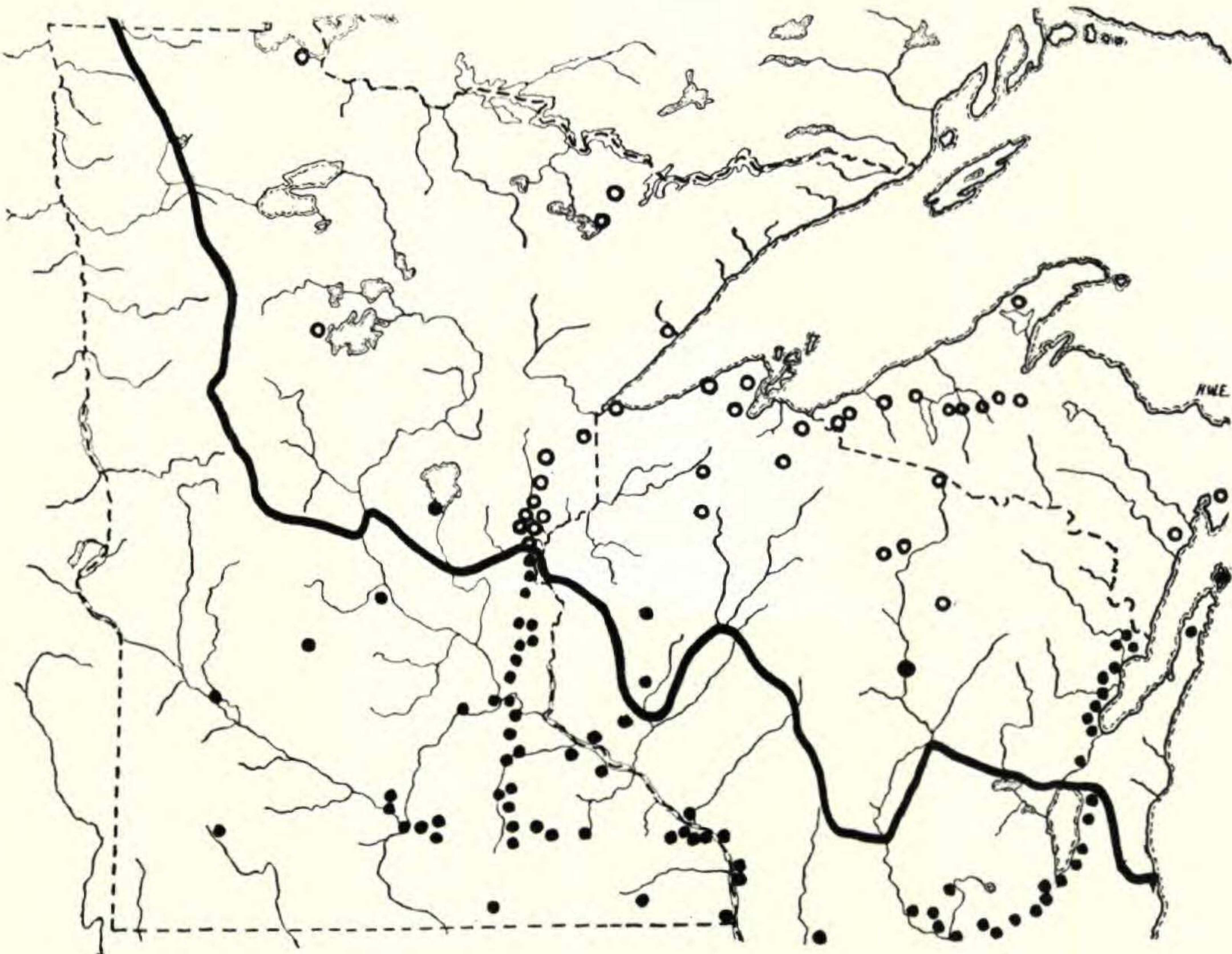


Fig. 1. Distribution of *IRIS VERSICOLOR* (open dots) and *IRIS VIRGINICA* (solid black) in Minnesota and Wisconsin. The irregular black line marks the approximate southern limit of the coniferous forest.

Although *Iris versicolor* and *Iris virginica* occupy very different ranges, they are found, one in the north and the other in the south, in almost exactly the same situations. They occur along the borderlines of swamps in the transition zone where it is too dry for *Typha* and too wet for grasses. So characteristically are they found in such situations that Gates in his studies of plant associations in Northern Michigan (1926) has named this transition zone the "Iris association."

In the rare cases where their ranges overlap, both species are found

growing side by side in the same wet pasture or along the same interdunal swamp. *Iris versicolor*, to be sure, shows its northern heritage in that it flowers earlier and ripens its fruits more quickly than does *I. virginica*. In those parts of Michigan where the two species grow together their blooming periods barely overlap. If there is any apparent difference between the requirements of the two species it is that *I. versicolor* is more tolerant of occasional drying out and can continue to flower and fruit in situations where *I. virginica* will only persist vegetatively.

In Michigan the habitats of the two species are particularly similar. Both in the northern and southern parts of the state there are numerous "tamarack swamps" filling poorly drained hollows left by the last glaciation. They seem to be fundamentally the same plant-association in all parts of the state, yet in the northeastern third of the peninsula, *Iris versicolor* is found about the swamp margins while in the south and west *I. virginica*, and never *I. versicolor*, is found in the same relative position.

Why should we find *Iris virginica* all the way from the gulf northwards, in cypress swamps, willow thickets, floodplain lakes, wet prairies, and sphagnum bogs, only to have it completely replaced by another and very similar species in the northern coniferous forest? Must it not be that the main reasons for the present distributions of the two species are historical rather than edaphic; that we find one in the northern Michigan swamps and the other in southern Michigan swamps, not because there is any great difference between the two situations but because one species has come in from the north in company with a whole northern flora and that the other has spread in from the south? It furthermore seems quite possible that neither species has moved about a great deal locally since it first entered the region. The one natural mode of travel of each species is by water. Their seeds and rootstocks float readily and are often found establishing themselves on marshy spots along lake and river beaches. There seems little possibility of spread by other means. The seeds are too large and heavy to be blown about. The rootstocks are acrid and poisonous and would seldom be carried by animals.

For the above reasons it was thought that the present distribution of the two species might quite accurately reflect ancient vegetational changes. A careful study of their exact distribution in northern Michigan was made in July 1931. Previous work had shown (Ander-

son 1928) that *Iris virginica* is found south of a curved line running from Tawas City, Michigan to Traverse City, Michigan, and that *Iris versicolor* occurs from there northwards. The 1931 field work confirmed this distribution with one surprising exception. As is shown in FIGURE 2 there is a large irregular area at the very tip of the peninsula where *Iris virginica* is found almost exclusively.

This anomalous distribution of *Iris virginica* is related in no apparent way to soil conditions or climatic factors. Douglas Lake and Munro Lake, for instance, are only one mile apart. Yet swampy land along the former is colonized by *Iris virginica* while in exactly the same relative locations on the edges of Lake Munro, *Iris versicolor* is common and prolonged search failed to reveal a single plant of the other species. Most of the situations in which *Iris virginica* is found in this area are ancient beaches of the glacial and post-glacial Great Lakes. Since both *Iris versicolor* and *I. virginica* are found coming up today along marshy beaches of the modern Great Lakes, it seemed possible that there might be some correlation between the distribution of the two species and the shore lines of these ancient lakes.

FIGURE 2 shows how very logical their distribution becomes on that assumption. Lake Algonquin, the last of the glacial lakes, persisted some time in the region and cut strongly marked beaches by which its extent can be accurately determined (Leverett and Taylor). These beaches show that in Algonquin time, northern Michigan was an archipelago of islands as is shown in FIGURE 2. Today those parts of the region which were then above the waters of Lake Algonquin are populated with *I. versicolor*. Throughout this whole area only one small plant of *Iris virginica* has been found above the Algonquin beaches and it was growing in a roadside ditch. *Iris versicolor*, on the other hand, occurs in profusion around Lake Munro and Lark Lake and in smaller quantities at several other points.

Below the Algonquin Beach line the situation is reversed. *Iris virginica* is found by the hundreds of thousands of plants and *Iris versicolor* is found only immediately below the Algonquin beaches, in situations where it might easily have been washed down from above, or as an occasional plant here and there along the roadside. The water level fell from the Algonquin to the Nippissing stage by a series of intermediate steps, leaving many abandoned interdunal swamps. In these swamps *Iris virginica* is found in enormous numbers. Around French Lake it occurs by the acre; in all the swamps

around Douglas Lake it is common and in some of them is associated with other southern plants such as Silver Maple (*Acer saccharinum*).

Near the edge of the Jack Pine Plains, a few miles south of the town of Indian River (on Burt Lake) is a wet meadow so similar to such formations in the south that one can find no better term to use in describing it than savannah. This interesting locality was discovered

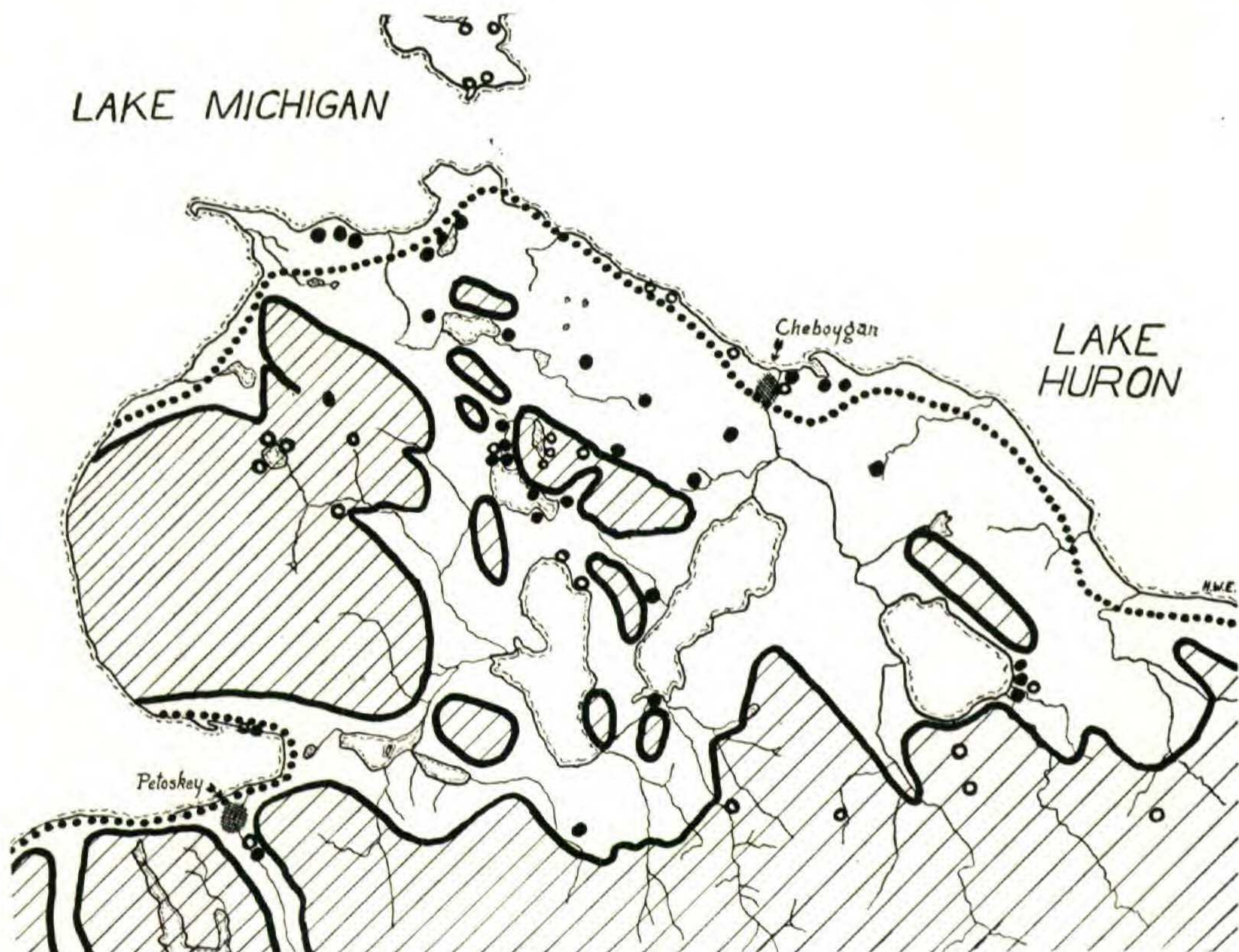


Fig. 2. Distribution of *IRIS VERSICOLOR* (open dots) and *IRIS VIRGINICA* (solid black) in the Douglas Lake region. The heavy black line represents the Algonquin beaches and the cross-hatched areas were above the waters of Lake Algonquin. The chain of dots represents the beaches of Lake Nipissing.

by Dr. J. H. Ehlers who has reported (1921) on the surprising occurrence there of the distinctively coastal plain species, *Panicum virgatum* L. var. *cubense* Griesb. Along the small stream which drains the area *Iris virginica* grows rampantly, its flowers borne nearly shoulder high. As one stands in the midst of the little savannah, surrounded by *Iris virginica* and *Panicum virgatum* var. *cubense*, and with the Jack Pine too far in the background to reveal their specific identity . . . it is hard not to believe that one is in the

Carolinas instead of at the edge of the Jack Pine Barrens of northern Michigan.

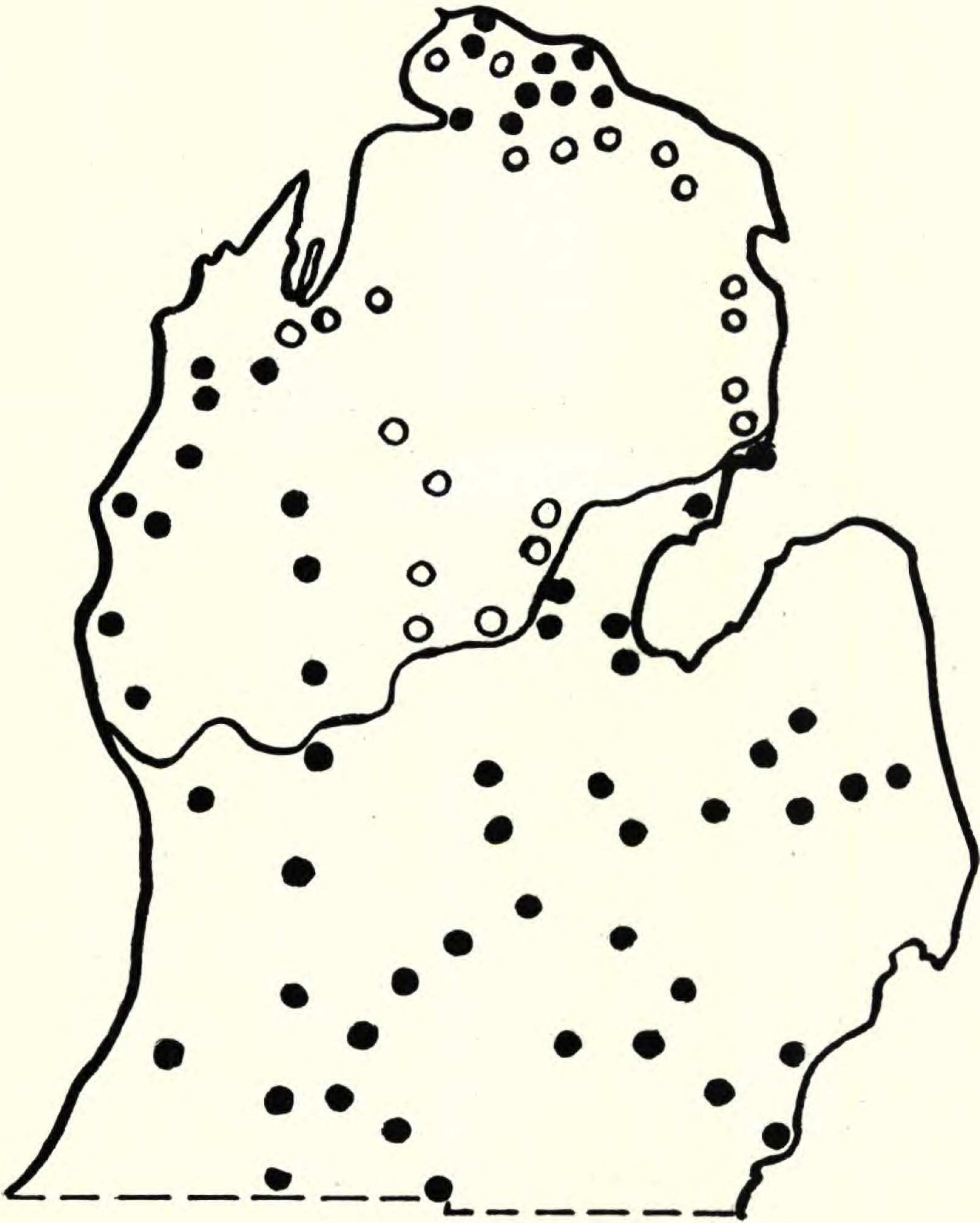


Fig. 3. Distribution of *IRIS VERSICOLOR* and *IRIS VIRGINICA* in the southern peninsula of Michigan. The wavy black line represents the approximate southern extent of the northern types of forest.

From the Nippissing level the Great Lakes fell to approximately their present level. Along the interdunal swamps of the intermediate levels both species are found, though *Iris versicolor* is apparently the more common.

Since *I. versicolor* is prevailingly a northern and *I. virginica* a characteristically southern species one might suppose that during warm eras *Iris virginica* would be brought to the lake beaches while during colder periods *Iris versicolor* would predominate. On these assumptions the present distribution of the two species would indicate; I. That in Algonquin time the mainland and the archipelago were clothed with a northern vegetation. II. That the waters fell from the Algonquin level during a time when the climate was much warmer, perhaps even warmer than it is at present, as evidenced by the almost complete absence of the northern species of *Iris* from the beach swamps of that period.

If these conclusions are confirmed by the pollen analysis studies of Michigan bogs already under way (Sears, 1930), the distribution of *Iris virginica* and *Iris versicolor* may prove useful in studies of glacial and post-glacial vegetation. The southern limit of *Iris versicolor* in Michigan (FIGURE 3) seems, for instance, to be correlated with the interlobate moraine of the last glaciation. Does this perhaps mean that *I. versicolor* persisted in the tundra vegetation of the interlobate region during the end of glacial times and that in the warm period following the retreat of the ice the regions previously covered by the Saginaw and Lake Michigan lobes were colonized by southern species?

In addition to the regions mentioned above, the two species meet in southern Ontario, north-eastern Ohio, to a certain extent at least along the Great Lakes-St. Lawrence system in New York, and on the Atlantic Coast. I shall be glad to assist anyone who may be interested in following up the minutae of their distribution in these regions.

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ARNOLD ARBORETUM.